Late Mid Devonian *Sawdonia* (Zosterophyllopsida) From Venezuela

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Abstract

Premise of research: Fossil plants from the Late Middle to early Late Devonian age Campo Chico Formation, Sierra de Perijá, western Venezuela, are determined to represent a new species of the zosterophyll genus *Sawdonia.* While mentioned in previous publications, this plant has not been previously described or formally named. A conclusive taxonomic assignment was not possible until clarification of the sporangial morphology of the type species of *Sawdonia*, *S. ornata* (Gensel and Berry 2016) from the Early Devonian of Canada.

Methodology: The adpressions were prepared, using dégagement, including serial dégagement and photography at each stage. Permineralized remains were prepared using established techniques for pyrite sectioning and polishing. Taphonomic analysis included preparing models and subjecting them to compression to aid in understanding their shape and orientation in life.

Pivotal results: The Venezuelan plants are adpressions of spiny axes that exhibit two types of branching (especially in vegetative ones), circinate tips, anatomy with G-type tracheids, and lateral sporangia with unequal-sized sporangial valves, the abaxial valve being spinous as is characteristic of the genus *Sawdonia* Hueber emend Gensel and Berry 2016. Sporangia are irregularly arranged along some axes and appear to be located in medial to subdistal regions. Spores were not obtained.

Conclusions: Differences in length and density of spines, the presence of two types of branching related to its growth habit, and details of sporangial morphology distinguish the Venezuelan plants from those of the type species and *S. deblondii*, thus leading to establishing a new species. This discovery demonstrates the longevity of the genus (ca. 20 million years) during a time of profound vegetational change, including the rise of forests, and is the first record of a fertile zosterophyll recorded from the Middle Devonian of South America.

Introduction

The late Silurian to Devonian (c. 430-360 Ma) was an interval of profound global transformation, much of which was driven by the emergence of vascular land plants. At first these plants were small, but their height and girth progressively increased until the rise of the first forests in the Middle Devonian Epoch (c. 390 Ma). Reconstructions of Middle to Late Devonian trees and forests have become increasingly well known (e.g. Giesen and Berry 2013, Berry and Marshall 2015, Stein et al. 2007, 2012), supported by impressive fossil discoveries. However the smaller plants of the Middle to Late Devonian have been less celebrated, and their role in ecology dominated for the first time by much larger plants as yet downplayed.

The subdivision Zosterophyllopsida (*sensu* Kenrick and Crane 1997), members of which are commonly called zosterophylls, is composed of numerous genera, most of which occur in the Late Silurian to Early Devonian. The plants consist of creeping or rhizomatous and upwardly-growing stems, and range in size from a few cm to decimetres in height. Globose to reniform sporangia are attached along the sides of axes in a variety of patterns. Some taxa are ornamented with emergences, varying in shape and/or arrangement. Several taxa exhibit circinately coiled stems and some show rooting structures (Gensel et al. 2001; Kotyk and Basinger 2000). While the earliest zosterophylls occur in the Ludlow (late Silurian), and along with the lycophyte B*aragwanathia* Lang et Cookson and *Cooksonia* Lang represent some of the earliest vascular plants, the group became very diverse in the Pragian (mid Early Devonian) in several regions (Cascales-Miñana and Meyer-Berthaud 2013), especially China (Hao and Xue 2013). Zosterophylls remained common components of Emsian (late Early Devonian) assemblages in Laurussia, Gondwana, Siberia, and China.

Only a few detailed reports of genera in younger strata exist, the most established being those of *Serrulacaulis* from several localities in the Middle Devonian of Belgium,

Venezuela, and China, and the early Late Devonian of New York State (Stockmans 1968; Berry and Edwards 1994; Xu et al. 2011; Hueber and Banks 1979). Hueber and Grierson (1961) identified vegetative axes with preserved cuticular features as *Psilophyton princeps* var. *ornatum* (= *Sawdonia ornata*) from the Frasnian (early Late Devonian) of South Mountain, New York State, but following the re-study of material of *S. ornata* from the type locality in Gaspé and redefinition of the genus and species, these specimens currently are suggested as *cf. Sawdonia sp*. (Gensel and Berry 2016). All established Mid-Late Devonian zosterophylls exhibit multicellular emergences, circinate tips and where known, sporangia arranged along the axes, thus being more closely allied to Sawdoniacae of Kenrick and Crane (1997) than to other zosterophyll types. Where present, usually one or two taxa occur, often in association with much larger vegetation, including trees known to grow in forests. Equally interesting is that the zosterophyll genera present in these younger strata appear very similar to the earlier ones, suggesting both morphological stasis and adaptability to dramatically changing vegetation structure.

Here we report a new occurrence of a late Middle Devonian age zosterophyll exhibiting fertile and sterile characters that allow attribution to the genus *Sawdonia* as a new species, definitively demonstrating the longevity of the genus and confirming its presence in the Mid-Late Devonian. Fossils are complete enough to suggest a reconstruction of overall habit. In addition to their importance as components of these younger floras, their presence further enhances similarities between plant assemblages from uppermost Middle Devonian strata in Venezuela and lowest Upper Devonian strata of New York State.

Materials and Methods

Well preserved Devonian plant fossils were first described from the Campo Chico Formation, in the Sierra de Perijá, Western Venezuela, by Edwards and Benedetto (1985).

The present fossils were collected by C.M. Berry, Dianne Edwards, John Moody and Johnny Casas from localities 3a and 3b of Berry et al. (1993) (updated map is shown in fig. 1 of Berry and Edwards 1996a) which are two exposures of the same horizon on the 'Old Road' located about 5 m from one another. This horizon represents the oldest diverse plant assemblage above the base of the Campo Chico Formation. Underlying brachiopods, in the marine Caño del Oeste Formation, indicate a Middle Devonian (Givetian) age (Benedetto 1984). Stratigraphic palynology has been studied by Harvey (2001). The Caño del Oeste Formation exposure on the Old Road, estimated to be 40-50 m stratigraphically below plant fossil locality 3, shows the first record of *Samarisporites triangulatus*. Harvey's overall analysis suggested that locality 3 is placed in the *optivus-triangulatus* spore zone (late Givetian to earliest Frasnian) of Richardson and McGregor (1986), and probably quite low in that zone, with the overlying *ovalis-bulliferous* spore zone (early but not earliest Frasnian to mid-late Frasnian) not identified until near the base of the overlying New Road section (approximately locality 8 of Berry et al. (1993)). Therefore the *Sawdonia* horizon is most likely of late Givetian age, although an early Frasnian age cannot be completely ruled out.

Sediments are a green-grey to green-yellow siltstone to fine sandstone, with local red iron staining. Sedimentary particles are large enough that epidermal patterns of stem or sporangium are unclear. Specimens were originally prepared and studied as part of the PhD dissertation of C.M. Berry (1993), and new preparations have subsequently been made by both authors. The fossils are preserved as adpressions, with much of the carbon adhering to axes or sporangia being very highly coalified such that neither cuticle nor spores could be obtained. With the exception of a few specimens, they consist of short lengths of axes that occur intermixed with other plant types, in particular sterile and fertile appendages and short branch segments of the arborescent pseudosporochnalean cladoxylopsid *Wattieza casasii* (Berry 2000, Stein et al. 2007), the iridopteridalean *Compsocradus laevigatus* (Berry and

Stein, 2000), the herbaceous lycopsids *Haskinsia sagittata* (Edwards and Benedetto 1985, Berry and Edwards 1996a) and *Colpodexylon cachiriense* (Edwards and Benedetto 1985, Berry and Edwards 1995), and the zosterophyllopsid *Serrulacaulis* cf. *S. furcatus* (Berry and Edwards 1994). Some aneurophytalean progymnosperms and other plants occur that have not yet been studied. Also present in the Campo Chico Formation, but higher up in the sequence, are the iridopteridalean *Anapaulia moodyi* (Berry and Edwards 1996b), the herbaceous lycopsids *Leclercqia* cf. *complexa* (Berry 1994), *Colpodexylon coloradense*, *C. camptophyllum* (Berry and Edwards 1995) and *Gilboaphyton griersonii* (Berry and Edwards 1997), and the progymnosperm *Tetraxylopteris reposana* (Hammond and Berry 2005). The exact sedimentary environment is unclear, but plants indicate burial close to the site where they grew, with fluvial systems producing overbank deposits on a delta plain (Berry et al. 1993).

Preparation techniques included dégagment to uncover plant parts using sharpened tungsten needles (Fairon-Demaret et al. 1999); in some cases each stage of serial dégagement (especially of sporangia) was recorded photographically and by camera lucida drawing, allowing interpretation of some very three dimensional but highly distorted specimens. Photographs were taken using cross-polarizing light to increase contrast (Rowe 1999). Plasticene models of sporangia were created and squashed or distorted in order to better understand and "retro-deform" to original shape and orientation. Macerations for cuticle and spores were attempted, with no success. One specimen exhibited permineralized regions, mostly in limonite, along an axis; these were removed, embedded, and polished sections prepared. Polished surfaces were studied by reflected LM (Kenrick 1999) and SEM. Plates were prepared in CorelDraw vers.18, with minimal alteration of color and contrast. Type and figured specimens are deposited at the National Museum of Wales, Cardiff (prefix NMW).

SYSTEMATICS

For higher order taxonomic ranks, we follow Kenrick and Crane (1997). Comparisons among the three now recognized species of *Sawdonia* indicate that a slight emendation of the generic diagnosis is needed in regard to nature of the sporangial dehiscence region.

Division Lycophyta

Class Zosterophyllopsida

Order Sawdoniales

Genus *Sawdonia* Hueber emend Gensel et Berry 2016 emend

Emended diagnosis (significant change in italics): Stems pseudomonopodially branched, circinately tipped, unridged and spinous; the spines tapered, pointed; epidermal cells with cuticular papillae; stomata on stem but not on spine surfaces. Sporangia round in abaxial view, splitting into unequal valves; larger abaxial valve more convex, smaller adaxial valve flat in lateral view; sporangia borne laterally and singly on short stalks, in one to two rows, in subdistal and distal regions of axes, without subtending organs; stalk extends at least half the length of the abaxial valve, merging with it; spines occur on abaxial surface of stalk and abaxial valve; dehiscence of sporangium transverse, basipetal, revealing narrow dehiscence margin*, level with sporangium wall* or inwardly folded, on both valves; apparently homosporous.

Type species: *Sawdonia ornata* (Dawson) Hueber emend Gensel et Berry (2016)

Holotype: Museum Specimen Number 3243 (Dawson 1871, Plate IX, fig 101); Peter Redpath Museum, McGill University, Montreal, Québec, Canada. Sir William Dawson Collection.

Epitype: Geological Survey of Canada GSC 138217 (Gensel and Berry 2016).

Sawdonia hippotheca sp. nov. Berry et Gensel

Figures 1-11

Derivation of name: From the Greek ίπποσ (hippos) - horse and θηκη (theke) - case, container, referring to the horse's-head appearance of some of the sporangia.

Holotype designated here: NMW 93.97G.49a and counterpart 49b, Fig. 2D, E

Paratypes designated here: NMW 93.97G.50 i-iii, Fig 1A, D, E; NMW 93.97G.58, Fig. 3G.

Locality: 3 of Berry et al. 1993.

Horizon: Green sandstones near the base of the Campo Chico Formation, Devonian, probably late Givetian

Diagnosis: Aerial axes 1.0-5.6 mm wide (x = 3.9, n = 97), predominantly pseudomonopodially branched with occasional K-branching. Branching type 1 - secondary axes arranged alternately in a planar branch system, some with abaxial projections close to branching point; secondary axes depart from straight primary axes at a wide angle and bend upright to lie parallel with primary axes or remain curved and dominant, branching is often alternate; most axes terminate in circinate tips, short lateral axes with rounded terminations. Branching type 2 – includes wider angles of branching with short extensions of the main axes terminating in a circinate tip, longer lateral branches, sometimes short basally bifurcate lateral branches, K-branches, and narrow, short, spineless lateral axes. Spines cover most axes, 1.5-5 mm in length, of variable density. Sporangia 2-4 mm wide, 1.2-3 mm high, with unequal valves, arranged in a single row or two almost opposite ranks; larger valve deeply convex with long spines, smaller valve nearly flat and lacking spines; sporangia with transverse dehiscence, sporangial valve margins slightly thickened to form a rim level with valve wall. Sporangial stalk up to 1.3 mm wide at base, tapering, short. Xylem strand elliptical,

haplostelic, xylem cells with close-spaced annular thickenings, pitlets in wall between thickenings (G-type).

General morphology

The morphological description is based on about 100 axes on 30 slabs. The specimens consist of varying lengths of spiny axes, ranging from 1.0-5.6 mm wide, the majority being 4-5 mm wide. Most of the axes are straight or slightly curved (Figs 1, 2). Those that are not show signs of having been broken prior to burial or disturbed during compression. Axes are either unbranched and incomplete at both ends or more extensively preserved and branched. The longest unbranched axis is 10.5 cm long (Fig. 1L), while the longest branched one is at least 20 cm long (Fig. 1A). Axes, where not broken distally, often have a circinate tip (Fig. 1D, E, J; Fig. 2G, H). The available specimens include three large axis systems lying on one block in almost the same plane (Fig. 1A, D, E, I) that provide considerable information from which to infer disposition of different parts of the plant.

For any individual, all branches lie in the same plane, there being no overlap or wedges of matrix suggesting an original three-dimensional organisation for the plant. Although branching is dichotomous, the varied angles and ongoing trajectory of the branches following a dichotomy, described below, leads to a distinctive overall architecture of upright parallel axes which we interpret for much of the plant in life (branching type 1). A second mode of branching (branching type 2), evident in some specimens, exhibits more frequently branched axes, some often partly or completely circinately coiled. In all, lateral branches are either alternately or irregularly arranged. The entire aerial branching system is thus considered to be planar and pseudomonopodial. Details are presented below.

Branching type 1

At the point of dichotomy, the lateral branch diverges at a broad angle (up to 90 degrees) from the main axis, which usually continues in its original direction, and the lateral then curves upward to become parallel or subparallel (Fig. 1A; Fig. 2B, D, E). Often the daughter branches are equal in diameter, but this is not always the case. In most examples one member of the dichotomy remains relatively undeveloped- e.g. as a bump (?bud) (Fig. 1K), a very short axis terminating in a rounded tip (Fig. 1A), or a short axis terminated by a circinate tip (Fig. 2G, H). One or both of these daughter axes may dichotomize up to two more times, repeating the pattern (e.g. Fig. 1A; Fig. 2B).

Much of the observed variation in branching patterns can be seen on the largest specimen (NMW 93.97G.50 i, Fig. 1A). The main axis is straight at the lowest branching-point, at which a very slightly narrower lateral branch departs on the right at an angle of about 45° from the upright. This lateral branch curves at the base to become subparallel to the main axis. The main axis (*M*), to the left, extends approximately 9 cm further, and is broken at the tip. A short undeveloped lateral is seen departing from the left side of it (Fig. 1A, left arrow). The right lateral axis extends 18 cm longer before ending at the edge of the block. It produces three alternately arranged lateral branches at 3-5 cm intervals (Fig. 1A, *1-3*). The proximal two are undeveloped, but the third is extended and itself divides to produce an abaxally curved lateral axis. That lateral extends 20 mm and divides again in the same manner. Both are truncated at the edge of rock, with the left-hand branch suggesting another division just before the edge.

A second specimen, NMW 93.97G.55, part and counterpart (Fig. 2B), together show an approximately 17 cm length along which three divisions occur. Proximally, the axis forks, emitting an initially twisted, but later untwisted, long lateral daughter axis. This axis branches twice more to form three sub-parallel distal axes.

A different, shorter axis demonstrates a bifurcation, where the narrow lateral axis becomes nearly parallel, but then curves back over the other axis and ends in a circinate tip, the curving most probably a result of preservation (Fig. 2G). A second example with a circinate tip on the lateral branch has both axes more equal in diameter (Fig. 2H).

On the abaxial side of some lateral branches at a distance of c. 4 mm from the branching point, a small lump or more extended spine-like feature is present (Figs 1A – right arrow, K).

Branching type 2

The disposition of branching axes in several specimens varies from the pattern described above, showing wider branching angles which do not end up subparallel, short blunt-tipped laterals laterals that may be basally dichotomous, and short thin axis extensions which lack spines.

In specimen 93.97G.50 ii (Fig. 1D), at the most proximal preserved part a division occurs and a 7 mm wide axis 10 mm long departs at an acute angle and forms a short, sharply curved axis which is broken at its tip (no crozier present). Approximately 5 mm along the curved axis, a small lateral branch departs to the left, but is preserved for only a short distance (Fig. 1D - arrow). About 25 mm along the presumed main axis (Fig. 1D – *M*), a long lateral branch departs nearly perpendicular to the main axis, bends towards the main axis, and continues at an angle, whilst the main axis itself continues for 25 mm and terminates in a broad circinate tip. The long lateral branch bears further short lateral branches about 20 mm apart (Fig. 1D – *1*-*3*). The first (*1*) is complex; it appears to bifurcate with a left daughter axis which is either broken off, rounded, or is a downwardly bent circinate tip, and the right one apparently dividing unequally to form a small circinate tip to the left and a longer thin spineless axis terminating in a curled tip to the right (Fig. 1B). The surface of this bifurcate

branch is wrinkled and at least in part covered in small dense spines. The more distal short lateral branch with a broadly rounded tip (Fig. 1D - *2*) is similar to those previously noted on the largest specimen. The third (*3*) is narrower. The distal end of the axis is curled tightly into a poorly preserved circinate tip.

Specimen 93.97G.50 iii (Fig. 1E) also displays a branching pattern with the main axis (*M*) forming a shorter, broad circinate tip (left) and the longer lateral axis departing at a wider than normal angle. In this case the lateral axis is quite strongly curved. The first appendage from the lateral axis (*1*) can be demonstrated to be bent or curved back across the axis on the counterpart (not shown). The second lateral appendage (*2*) divides into two, and the ends of these short branches appear to terminate abruptly although a sheet of red mineral matter in a fissure makes convincing interpretation of these structures impossible. The third and fourth lateral appendages (*3*, *4*) are short, and broken at the tip. The fifth lateral appendage (*5*) is short and straight, but again mineralisation has badly affected this end of the fossil.

Axis 93.97G.51 i (Fig. 1F) exhibits a lateral which extends a short distance and then dichotomizes, forming two widely spread apart axes as a K-branch (Fig. 1H). Spines are visible except at the tapered distal ends of these axes and they curve, one back towards the major axis (Fig. 1H). Both end in blunt tips. Further along the axis, near where preservation ends, the main axis narrows and two laterals depart, each at a broad angle. These lack spines and taper from about their mid-region to the slightly rounded tip (Fig. 1G). They are very different in form and disposition to any other laterals. This part of the main axis has very small spines only on the side opposite the laterals, and terminates in a small narrow spineless axis that appears to have a circinate tip. A further example of a K-branch, on a very short length of preserved main axis, shows the lower lateral branch bifurcating (Fig. 2F - arrow).

In summary, specimens show a plant consisting of dichotomizing axes in which two types of branching are seen. One involves an uninterrupted straight axis with a curved lateral

axis that straightens to become subparallel to the main axis; this is the most common branching pattern observed in more fragmentary material. On some examples the side branch is markedly narrower and ends circinately curled in an abaxial direction. The second shows presumed major axes which after division are more curved and spreading, with some laterals extending longer than in the major axis; the latter ending in a circinate tip. Two other types of lateral branches, one forming a K pattern and one which is short and straight but tapers distally, are distinctive (see discussion of growth habit).

Spines

Long spines occur fairly densely on most axes, being most densely placed at circinate tips (Figs 1, 2). They are clearly visible along sides of axes, and spine bases of well-preserved axes are represented by a slight depression on the surface of compressions (e.g. Fig. 1K). Where clearly visible, axial spines vary in length from about 3-5 mm, being largest and most separated on larger axes, with occasional ones being smaller. Spines are smallest and most closely packed around circinate tips and small axes (Fig. 1B, G, J). On the abaxial valve of the sporangium they are approximately 2 mm long. Spines are widest (0.6-1 mm) at their base. They taper sharply for a short distance above the base to half that width and then taper more gradually to a fine point (Fig. 1C, L). The bases are decurrent, some being symmetrical on both upper and lower sides and others only upwardly or downwardly asymmetrical. On some branching specimens it can be demonstrated that, although a decurrent base is prevalent, the more broadly decurrent spine base may run upwards rather than downwards. It is therefore impossible to orientate unbranched stems with certainty using the bases of the spines. It has not yet been possible to demonstrate cuticle on stems or spines. The matrix is too coarse to determine outlines of epidermal cells, stomata or papillae from impressions.

Fertile specimens

A number of axes bear one to several small lateral organs. Those that show evidence of a well-defined rim are interpreted as fertile organs consisting of a thin-walled bi-valved sporangium and subtending stalk. These have a complex taphonomic history, are variously crushed, and so their appearance is highly varied. They are found open (dehisced) and are sometimes filled with sediment. What can be determined most clearly is outlined in the following section, and taphonomic variability is discussed in a further section below.

The most easily interpreted part of the fertile organ is the smaller, adaxial, sporangial valve, which is sometimes observed lying flat, nearly complete and only slightly folded (Fig. 3A, C, G, I; Fig. 4A, F; Fig. 5A-E). It is slightly broader than high, ovate to slightly reniform, has a distinct narrow rim demarcated by a very narrow thickening emphasised by carbon (Fig. 3C, Fig. 5F), and lacks spines. It is attached to the stalk (or can appear continuous with the stem surface) only at a narrow proximal zone (Fig. 3A, G; Fig. 4C, F), the rest of the valve margin being free.

In three specimens, the flat adaxial valve is observed inside the larger, abaxial, valve which is seen only in section, as the thin valve wall is here orientated perpendicular to the surface of the block (Fig. 3A, G – lower arrow; Fig. 4A – between arrows). The larger valve bears spines (e.g. Fig. 3G – upper arrow, Fig. 4A). Observations on all specimens, including those preserved as internal/external moulds (Fig. 3A-D, G) suggest that this valve is deeply convex. Serial dégagement (Fig. 5) demonstrates how extensively the abaxial valve can fold over the adaxial one during preservation.

The short stalk appears symmetrical and tapering in some views (e.g. Fig. 3E, Fig. 4E), but quite strongly curved in others (Fig. 3B, F). These views are consistent with a curved

stalk which is sometimes curled around the stem surface, and other times up or down the stem surface.

Sporangial position

Sporangia occur singly, alternately, or sub-oppositely mostly on shorter axes (Fig. 2A - arows, C; Fig. 6A - arrows), although several are present on one longer, branched axis (Fig. 2D, E - arrows). In the latter, sporangia are visible on both axes above, but none are visible below the bifurcation. Where in a regular pattern, the sporangia are arranged in one or two vertical ranks and with a vertical separation of between 8-12 mm. Given the incompleteness of the specimens it is difficult to determine if the sporangia are restricted to the upper portions of aerial axes or more scattered. The incomplete axis in Figure 2A shows more or less alternate sporangia below, and two subopposite ones at the upper end (also Fig. 6B), all in different orientations. Figure 2C shows an incomplete, fairly short axis in which one sporangium is oriented in one direction and another in the opposite direction (*1*, *2*), making it difficult in unbranched specimens to determine correct orientation of the axis. In specimen NMW 93.97G.49e, a short lateral branch with a closely coiled tip has one sporangium attached close to the base (Fig. 6C). The margin of the adaxial valve is visible between the margin of the larger abaxial valve and the branch (Fig. 6D - arrow).

Details and taphonomy of sporangia

Most sporangia are dehisced and the thin walls of one or both valves appear incompletely preserved, distorted, or torn apart, or the two valves have been spatially separated from one another (Figs 3-5), partly as a result of their maturity and partly a result of taphonomic processes. Apparent sharp outlines that suggest a margin often instead represent a fold or broken edge. Sporangial position in the rock matrix is variable such that some are

viewed mostly or partially from the side, while others show either the ab- or adaxial surface of part of the sporangium and/or stalk. These factors, plus lack of compression remains removable from the matrix, has made interpretation challenging in some cases.

Stalk

Sporangia terminate a stalk that is widest at the base (ca.1.3 mm) and appears to taper rapidly in some lateral views (Fig. 4E, Fig. 5E, Fig. 6C). The specimen in Figure 4E shows the broad-based stalk in adaxial view, approximately 0.8 mm long, with the convex abaxial valve bent towards it. Length of most sporangial stalks is difficult to determine for two reasons 1) the stalk grades imperceptibly into the sporangium, especially into the abaxial sporangial valve, and 2) both stalk and sporangium curve or bend, sometimes sharply (90-180 degrees) with it sometimes being unclear whether the bending is at the sporangium-stalk junction or somewhere on the stalk or sporangium (Fig. 6C).

Mould and cast

Two mould/casts are among the best preserved sporangia. The first (NMW 93.97G.57, Fig. 3A-D) lies some distance from the side of the axis to which it may have been attached. An example of an almost identical, yet attached sporangium preserved as mould/cast is seen in Figure 3G (NMW 93.97G.58).

The initial view of specimen NMW 93.97G.57 (Fig. 3A) exposed the adaxial valve in face view, the outer margin of which shows a very narrow but distinct dehiscence line around much of the margin. The larger abaxial valve was initially represented by only a thin line which represents a section through the abaxial valve at the level at which the matrix was split open. A small amount of it in the upper part of the photograph was revealed by degagement to have some depth into the matrix. It was therefore possible to 'pop' the sporangium out of the matrix to give an internal sediment cast of the sporangium (Fig. 3C-D) and reveal the inner surface of the far side of the abaxial valve and the stalk (Fig. 3B).

The proximal margin of one half of the lateral dehiscence line on the abaxial valve is visible as a strongly-curved margin which is lost at the edge of the internal cast (Fig 3D, white arrow) where it joins the broken wall of the formerly exposed upper part of the abaxial valve (Fig. 3A, B – white arrows). The stalk is curved and in this view does not appear to be obviously tapered (Fig. 3B, D).

A second equally well- preserved mould/cast of a sporangium (Fig. 3G, NMW 93.97G.58) is oriented nearly vertically at the side of an axis and with part of the sporangium viewed from the adaxial surface. It shows the adaxial valve and a section through the abaxial valve (Fig 3G – lower arrow) with part of a spine (upper arrow).

Somewhat distorted, but almost complete compressed sporangia

At the distal end of NMW 93.97G.51 i (Fig. 2A, Fig. 6B) two subopposite sporangia occur on an axis; the one on the left is bent towards the axis, showing a very curved abaxial (outer part) valve and perhaps part of the adaxial valve, and the one on the right exhibits an adaxial view of that sporangium. Serial dégagement of the latter (Fig. 5) demonstrated that the adaxial valve was folded, and could not be exposed flat, crushed inside the very convex adaxial valve. On axis NMW 93.97G.49b iii, one unusually folded and perhaps split abaxial valve (Fig. 3H), was partially removed by careful dégagement to reveal the flat adaxial valve inside (Fig. 3I). Another sporangium (Fig. 3J) on the same specimen also shows the adaxial valve nearest the axis (below) partly surrounded by the edge of the abaxial valve (and base of a spine). Each of these three sporangia show very different aspects depending on the orientation of the organ with respect to the viewer, the crushing, folding and probably tearing of the very thin abaxial valve, and the level in the matrix they were exposed.

Stalk/sporangium in partial side view

The sporangia in Figures 3E, F show part of the stalk and an abaxial valve with two spines or spine bases; the abaxial valve is bent towards the axis in each case, but in different orientations and the adaxial valve is not visible. What appears to be most of the outer surface of an abaxial valve, almost completely folded back against stalk and axis, is shown in Figure 4D; the bases of two spines are visible on the outer margin of the abaxial valve, and arrows point to the edge of the valve. The sporangial portion of the specimen in Figures 6C, D, also shows a partial side vew of sporangium and valves; in this case, the adaxial valve margin is visible outside the abaxial valve.

Stalk/sporangium in ab- or adaxial face view

The abaxial valve of the sporangium in Figure 4A is represented only by a narrow margin, including part or all of its rim and attached spines (between arrows) whilst the clearly defined adaxial valve lies within it (the majority of the abaxial valve is presumed to have remained on the unavailable counterpart or beneath it in the matrix).

The sporangium in Figure 4B, while it appears to be preserved in mostly side view, is, on closer inspection, showing mostly a face-view of the concave abaxial valve from the inside; the outer rim with six attached spines located on that part of the abaxial valve is visible (interpretation in Fig. 7). Remnants of a possible stalk also occur.

A ventral view of two sporangial valves and part of the stalk of a sporangium lying behind an axis (Fig. 4C - centre) were revealed by serial dégagement. The two sporangial valves are slightly offset, with the rim of the adaxial valve (Fig. 4F - at arrow) and a narrow portion of its stalk is attached.

Summary of sporangial features

The above variations result in the following interpretations: 1) the sporangial stalk is broader at its base and tapers immediately, merging imperceptibly into the abaxial valve of the sporangium; 2) the abaxial sporangial valve is larger, very convex, with a narrow region folding onto the adaxial surface and edged by a distinct rim; 3) several spines up to 1.5 mm long occur on the abaxial valve of the sporangium, and apparently sometimes on the stalk; 4) a smaller, more flat adaxial valve with a distinct rim and a moderately broad base but lacking spines attaches to the stalk and abaxial valve; and 5) sporangial valves appear wider than high, elliptical to slightly reniform; and 6) the sporangium or sporangium/stalk complex folds towards the axis abruptly at some level- producing in some instances a "horse's-head" appearance (e.g. Fig. 3E). This may be how the sporangia were oriented when alive rather than being entirely a preservational artefact. The available evidence for the morphology of the sporangia is summarised in the partial reconstruction (Fig. 8).

Despite attempts to macerate sporangia, no *in situ* spores have been recovered.

Anatomy

Only one specimen attributable to this species was anatomically preserved (Fig. 9A). The specimen is poorly preserved, with only a thin carbon compression of the axes (4.6-6.1 mm wide), and spines were only just visible. Characteristic type 1 branching was present. The xylem column was preserved as a 1.0-2.0 mm wide three-dimensional strand along some of the visible axes, the dull red/brown colour indicating that limonite was the major constituent. Details of the gross anatomy were observed by reflected-light microscopy of four polished sections made from the limonite petrifactions where they became buried in sediment at the top of the specimen. The limonite is quite soft and so the quality of preservation is poor. The entire strand appears elliptical to strap shaped (Fig. 9B). The strand could be

elongated in preparation for division, and because of poor preservation it is not possible to establish unequivocally if the xylem column was terete or elliptical in cross section. The xylem observed suggested it was somewhat flattened. No small diameter xylem cells have been observed near the centre of the xylem where preservation is best and so it is likely that maturation was exarch. In transverse section, cell walls enclose a polygonal lumen (Fig. 9C). Some carbonized (or coalified?) cell walls appear broad, presumably where they form parts of thickenings. Others are thinner, and may be coated with reflective limonite. In places, small perforations in the black, non-reflective cell wall are visible (Fig. 9C - arrow). Many cells are distorted, crushed or badly preserved.

Limonite permineralisations were also placed directly on to SEM stubs (Fig. 10). Lumen casts, wall limonite and more rarely coalified secondary wall material are seen. Where coalified cell wall material is visible, it forms smooth, hollow C-section thickenings, separated by wall that is perforated by small holes or pitlets (Fig. 10C). This carbon is believed to represent the secondary cell wall. The primary wall cellulose is interpreted to be replaced by pyrite, now transformed to limonite (Kenrick and Edwards 1988a). This is seen both as sheets between adjacent secondary walls and also as ledges projecting towards the lumen, which represent the replacement of cellulose primary wall material which extended into the middle of the thickenings (Fig. 10B - right).

Lumen casts are the most visible form of preservation of the cells (Fig. 10A, B – left, D). Many lumen casts are hollow, seen both under the SEM and in polished sections. Lumen casts are generally smooth in the depressions formed by the thickenings, but between the thickenings are covered with small limonite lumps which have grown in the pitlets in the secondary wall (Fig. 10D), and which may have enlarged and distorted some of the pitlets. Thickenings are for the most part annular, but sometime bifurcations are observed (Fig. 10B - upper left). In some lumen casts the depression representing the thickening can be seen to

tunnel into the lumen cast and the surface of successive inter-thickening areas are joined by a smooth layer of limonite, pitted secondary wall or a shallower depression in limonite (e.g. Fig. 10D - arrow). This suggests that the thickening may be detached from the cell wall in some places for small parts of the circumference. Because of the thin secondary wall material which covered the annular thickenings, with pitlets occurring in the wall between the thickenings, the xylem cells described are identified as G-type (Kenrick et al. 1991).

Discussion

Comparisons and taxonomic determination

Gensel and Berry (2016) recently made the first descriptions of the sporangia of specimens of *Sawdonia ornata* from the type locality, leading to emendation of both the genus and species. *Sawdonia* sporangia exhibit unequal sized valves that occur along axes in medial and distal regions, and the larger abaxial valve is covered in spines - a major change in the concept of the fertile structures. Gensel and Berry suggested that the same organisation of sporangia was already known from *Ensivalia deblondii* Gerrienne (1996) from the upper Pragian of Belgium, and transferred the species to *Sawdonia deblondii*.

As a result of this new understanding, the authors suggested that apparently fertile specimens previously attributed to *S. ornata* from the Early Devonian of Canada (Abitibi River - Hueber 1971, 1992), Scotland (Rayner 1983) and Western Siberia (Ananiev and Stepanov 1968) should be considered as *cf. Sawdonia* sp. until all diagnostic features can be ascertained. Vegetative axes showing spines and epidermal features similar to *S. ornata* from the Early Devonian of Scotland (Lang 1932), the Witney Borehole, England (Chaloner et al. 1978) and Poland (Zdebska 1972), as well as those from the early Late Devonian of New York State (Hueber and Grierson 1961), also should at present be regarded as cf. *Sawdonia sp*. Gensel and Berry (2016) also suggested that plants attributed to the genus from Germany

(Schweitzer 1979, 1982), are of unclear affinity. *Sawdonia* from China is considered by Xu et al. (2011) as either too poorly preserved to be attributed to any taxon or they represent *Serrulacaulis.* *Sawdonia acanthotheca* (Gensel et al. 1975) requires a new generic designation, given its sporangial valves are nearly equal and spine morphology is highly variable (Gensel, personal observations).

The combination of characters demonstrated for the Venezuelan specimens suggest they are assignable to the genus *Sawdonia*. The short stalk and presence of two valves of unequal size, the larger abaxial valve, more convex and covered in spines, and the imperceptible transition from stalk into abaxial valve, are features of the Venezuelan plant that also occur in *S. ornata* and *S. deblondii*. Additionally, branching pattern, circinate unrolling of axes (stems), and tapered spines all around the axes are very similar to *S. ornata*.

A comparison of the three species we currently accept in *Sawdonia* is given in Table 1. The Venezuelan specimens differ from the type as follows: axes tend to be wider (range 1.0-5.6 mm in Venezuelan specimens with the majority 4+ mm wide vs. 1.6-4.5 mm in *S. ornata*); length of spines on both axes and sporangia in Venezuelan specimens, while overlapping in lower size range, is greater than most in *S. ornata* (up to 5 mm in Venezuelan plant vs. 3, occasionally 4 mm in *S. ornata*); the sporangial stalk is broader at its base and the stalk more robust where visible and measurable, and the abaxial sporangial valve is much more convex than that observed in *S. ornata*. It also appears that the modified dehiscence region of the two differ, that of *S. ornata* being wider and folded inward, and that of the Venezuelan plant appearing narrower and not folded. The formation of lateral branches, with a slightly smaller base departing almost perpendicular to the axis, then becoming parallel to it, and the presence of K-branching for the present time distinguish the Venezuelan plant from *S. ornata*. H-branching is recorded from cf. *Sawdonia ornata* from Scotland (Rayner

1983). Additionally the sporangia of the Venezuelan plant appear to have been at least partially bent towards the axis near the sporangium-stalk junction in life.

The Venezuelan plant also differs from *Sawdonia deblondii* (Gerrienne) Gensel et Berry 2016 in sporangial and emergence shape and size (Table 1). The abaxial sporangial valve in *S. deblondii* is more strongly reniform and not as deeply convex. Its stalk, while robust in comparison to *S. ornata*, is narrower than that of the Venezuelan plant. Shape of the spines differs in that those of *S. deblondii* have a broadly triangular base, taper rapidly and overall are much shorter than the more slender spines of the Venezuelan plant.

The plants from Siberia, England, Scotland, Poland and New York State originally referred to *Sawdonia* (or its earlier name *Psilophyton princeps* var. *ornatum*) and now regarded as *cf. Sawdonia* lack sufficient information about sporangial morphology or are based only on cuticular remains of stems. From what is known about them, they are more similar to *S. ornata* than the other two species, all differing in spine morphology from the Venezuelan plant. Thus we regard the Venezuelan specimens to be sufficiently different to constitute a new species of *Sawdonia*.

Postulated growth habit

Two styles of branching are shown by the Venezuelan *Sawdonia hippotheca*, which are important in our interpretation of the plant's growth architecture. Branching type 1 involves an aerial portion consisting of an uninterrupted straight axis with a curved lateral axis which straightens to become subparallel to the main axis; this is the most common branching pattern observed in more fragmentary material. On some examples the side branch is markedly narrower and ends circinately curled in an abaxial direction. Branching type 2 shows a major axis which after division produces daughter axes that are more curved and spreading, with some laterals extending longer than the major axis, which itself ends in an

abaxially circinate tip. Other laterals may be basally dichotomous. Short narrow naked axes may also be part of the type 2 system. Some of these apparently end in circinate tips, whilst others are tapering, and do not occur at K-branches, so whilst they therefore cannot be directly compared to, for example, the presumed roots of *Bathurstia* (Kotyk and Basinger 2000) they may have had some sort of anchoring function. K-branching is present in only two of our specimens.

We suggest that the type 1 branching pattern is typical of aerial, upright portions of the plant, and that this is also where sporangia are located. The best explanation of the several features distinctive for type 2 branching is that these may represent a basal, partly creeping, or rhizomatous (above-ground) portion of the plant, based on 1) the angle of departure and evident curvature which probably is not taphonomic, 2) one axis, most probably the main axis, at a dichotomy remains immature and the lateral branch extends for several decimetres, and 3) that most of the longer circinately coiled axes are to one side of the axis.

We offer a reconstruction of the plant based on these observations and interpretations in Figure 11.

Ecology

In Horizon 3 of the Campo Chico Formation, the *Sawdonia* fossils are found associated not only with the zosterophyll *Serrulacaulis* (Berry and Edwards 1994), but also the cladoxylopsid *Wattieza* (Berry 2000), the iridopteridalean *Compsocradus* (Berry and Stein 2000), undescribed anuerophytalean progymnosperms, and the herbaceous lycopsids *Haskinsia sagittata* and *Colpodexylon cachiriense* (Edwards and Benedetto 1995). While not autochthonous deposits, these hint at an emerging Mid Devonian forest ecology which may have had an interesting understory component as well as the large tree *Wattieza* and

recumbent aneurophyes as the dominant large plants, as at Gilboa, New York (e.g. Stein et al. 2012), so far the paradigm for a Mid Devonian forest ecosystem. This potentially contrasts strongly with the Lower Devonian (Emsian) ecology of type *Sawdonia ornata*, from Gaspé, Canada, where *Sawdonia* formed a monospecific autochthonous stand (Hotton et al. 2001) and vegetation is not storied. At the early Frasnian (earliest Late Devonian) South Mountain locality, New York, where the youngest sterile axes attributed to cf. *Sawdonia* occur, there are other taxa in common with Venezuela, including the type material of *Serrulacaulis furcatus* (Hueber and Banks, 1979), *Wattieza* (Stein et al. 2007) and *Colpodexylon* (Banks 1966). Here the tree progymnosperm *Archaeopteris* is also present (Carluccio et al. 1966). It is clear that *Sawdonia* managed to tolerate, or adapt to, changes in plant ecology and the emergence of trees over a considerable period of time (c. 20 Ma).

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Figure captions

Figure 1. *Sawdonia hippotheca* sp. nov. from Venezuela. Vegetative specimens.

A. The largest of three axes on the slab shown in Fig. 1I. Comparatively long axis with departing lateral that turns upright and is nearly parallel to main (*M*) axis (branching type 1). Further short or incompletely preserved laterals depart from the right-hand axis (*1-3*). Scale bar = 20 mm. NMW 93.97G.50 i.

B. Partly coiled, bifurcating lateral branch departing from axis shown in Fig. 1D (*1*), the first divisions coil downwards into matrix; one on right has divided again to produce a narrow, coiled narrow spineless axis extending to the top right. Note spines near the base. Scale bar = 5 mm. NMW 93.97G.50 ii.

C. A typical spiny emergence showing absence of a vein or darkened tip, close-up of Fig. 1D (opposite *M* centre). Scale bar = 2 mm. NMW 93.97G.50 ii.

D. Second large axis from slab in Fig.1I, showing branching type 2. At base left a short lateral that in turn branches (arrow), and ends in a circinately-coiled tip. Main axis (*M*), terminates in a circinately-coiled tip; it produces to right, a long lateral bearing three short axes (*1-3*) and terminates in a closely-coiled tip. Note slightly smaller base of the large lateral branch and its initial orientation at right angle followed by curving back. The bifurcating, coiled lateral (*1*), is shown in detail in Fig. 1B. Scale bar = 20 mm. NMW 93.97G.50 ii.

E. Third large axis from slab in Fig. 1I, showing branching type 2. The main axis (*M*) to left terminates in a circinate tip shortly after departure of a lateral. Lateral departs at right angle and terminates abruptly. Five axes depart from sides of this lateral (*1-5*), some short, one (*2*) bifurcated. On counterpart, axis *1* is extended and crosses back across the main lateral. Scale bar = 20 mm. NMW 93.97G.50 iii.

F. Axis, bent during preservation, producing a K-branch lateral (Fig. 1H) and distally two straight, naked, tapered laterals (Fig. 1G) and a circinate naked tip. Scale bar = 20 mm. NMW 93.97G.51 i.

G. The termination of the axis shown in Fig. 1F, showing the axis narrows, lacks spines, and gives off two tapering lateral branches and ends in a narrow, closely-coiled tip. Scale bar = 5 mm. NMW 93.97G.51 i.

H. Lateral axis displaying K-branching developed on axis shown in Fig. 1F, ending in partly-coiled tips. Scale bar = 5 mm. NMW 93.97G.51 i.

I. Large block containing the three major axes figured in Fig. 1A-E, and other taxa including a large branch fragment (top left) and sterile appendage (bottom center) of *Wattieza*, and fragments of *Compsocradus*. Scale bar = 100 mm. NMW 93.97G.50.

J. A circinately coiled axis fragment. Scale bar = 5 mm. NMW 93.97G.52.

K. Axis showing a lateral branch curving to upright, with bump (possible bud) at arrow. Scale bar = 20mm. NMW 93.97G.53.

L. Longest unbranched axis illustrating the morphological variation and different orientations of emergences. Scale bar = 20 mm. NMW 93.97G.54a.

Figure 2. *Sawdonia hippotheca* sp. nov. from Venezuela. Vegetative and fertile axes.

A. Portion of a fertile axis showing helically arranged, mostly distantly spaced sporangia plus two subopposite ones at top (arrows). Scale bar = 10 mm. NMW 93.97G.51 ii.

B. Long axis; lateral branch bifurcates two times after departure (branching type 1). Photograph of counterpart below white line is reversed. Scale bar = 20 mm. NMW 93.97G.55a, b.

C. Part of a fertile axis, note one sporangium on left oriented towards top of image (*1*) and one oriented towards the bottom (*2*) - location of apex unknown. Scale bar = 20 mm. NMW 93.97G.56a i.

D, E. Holotype. Part and counterpart of fairly long axis with a nearly parallel disposed lateral branch (left-hand branch in E); both axes bear irregularly arranged sporangia (arrows) above the departure of the lateral. Type 1 branching. Scale bar = 20 mm. NMW 93.97G.49a i, b i.

F. Short length of axis with K-branch in which the lower distal axis is just beginning to divide again at the edge of the specimen (arrow). Scale bar= 10 mm. NMW 93.97G.43 ii.

G. Axis fragment with a long lateral branch initially nearly parallel to axis and distally bent over the front of it, terminating in a circinate coil. Scale bar = 10 mm. NMW 93.97G.43 iii.

H. Main axis with a nearly parallel lateral that terminates in a circinate tip. Scale bar = 10 mm. NMW 93.97G.37b ii.

Figure 3. *Sawdonia hippotheca* sp. nov. from Venezuela. Details of sporangia showing various orientations and distortions.

A-D. Sediment-infilled sporangium *in situ*, and resulting cast and mould when removed. A. sporangium *in situ*, with part of the stalk visible. The adaxial valve is visible in external face view, and the strongly convex larger abaxial valve is only visible as a broken section around it, revealing mostly only the thickness of the sporangium wall, but at the top part, the depth of the sporangium has been uncovered. Note that much of the abaxial valve is missing, it would have been on the counterpart, which is not available. The arrow indicates the point at which the margin of the abaxial valve reaches the edge of the cast, and this point is also indicated in arrows on Fig. 3B-D. B. Mould (carbonized impression) of the far side of the sporangium when the sediment-filled cast was removed, showing carbonized region of abaxial valve, and the stalk. The C-shaped white line represents the only preserved part of the dehiscence

margin of the abaxial valve, the remainder being lost on the counterpart. C. Removed cast of sporangium, adaxial valve side to front, note it is vertically folded inward at the top (arrowhead). Light area represents matrix, behind which an outer portion of the abaxial valve is visible (top). D. Reverse side of cast, showing a small part of the abaxial valve (*ab*), and curved stalk. A, B. Scale bar = 2 mm. C, D. Scale bar = 1 mm. NMW 93.97G.57 and 57.1.

E. Side view of upwardly bent sporangium (see Fig. 2C – *2*) showing broadly decurrent base of stalk, outline of part of abaxial valve only, and two spines. Scale bar = 1 mm. NMW 93.97G.56a i.

F. Semi-side view of individual sporangium bent frontwards; abaxial valve with spines, including part of its margin, is visible. Scale bar = 2 mm. NMW 93.97G.49c.

G. Sediment-infilled sporangium attached to axis. Sporangium dehisced, surface and rim of adaxial valve uppermost in face view, section through abaxial valve (lower arrow) with base of one spine (upper arrow) to outside. Scale bar = 2 mm. NMW 93.97G.58 and 58.1.

H, I. Two stages in dégagement of sporangium bent towards an axis. H. Abaxial valve, split into two parts, folded unto axis, with a small segment of adaxial valve (arrow) visible. I. Left portion of abaxial valve and/or stalk removed, revealing much of the adaxial valve below. Scale bars = 2 mm. NMW 93.97G.49b iii.

J. Another sporangium folded towards the axis, abaxial valve with base of spine above (*ab*), partly covering adaxial valve (*ad*). Scale bar = 2mm. NMW 93.97G.49b iii.

Figure 4. *Sawdonia hippotheca* sp. nov. from Venezuela. Details of sporangia in different orientations.

A. Axis with sporangium twisted so adaxial valve preserved in the same plane as the axis. A narrow section through the abaxial valve (arrows) with several spines surrounds almost completely preserved adaxial valve. Scale bar = 2 mm. NMW 93.97G.59.

B. Sporangium in same orientation as Fig. 4A above, but with the adaxial valve missing, showing concave inside and narrow outer margin of abaxial valve, with five spines. See line drawing in Fig. 7. Scale bar = 2mm. NMW 93.97G.46 ii.

C. Axis with three sporangia exposed after dégaging through axis, and a fourth (arrow) on the right side of axis (detail in Fig. 4E). Scale bar = 10 mm. NMW 93.97G.56a ii.

D. Axis with a sporangium in which the abaxial valve is folded back unto the axis. Some of abaxial valve margin is visible (arrows), and two spines at top. Scale bar = 2mm. NMW 93.97G.49d.

E. Closeup of sporangium on right side of axis in Fig. 4C. Note broad base of stalk. Abaxial valve is bent so margin is parallel to the surface of the axis, adaxial valve not visible. Scale bar = 2mm. NMW 93.97G.56a ii.

F. Sporangium, consisting of two slightly offset valves, with adaxial valve on top, and part of the stalk that was exposed by dégaging axis seen in Fig. 4C. Arrow indicates margin of adaxial valve. Scale bar = 2 mm. NMW 93.97G.56a ii.

Figure 5. *Sawdonia hippotheca* sp. nov. fom Venezuela. Stages in serial dégagement of sporangium, with outline of axis and spines, shown at top of Fig. 2A and Fig. 6B. Photograph on left with adjacent interpretive line drawing based on tracing of images. Outer part of abaxial sporangium is shaded medium gray, adaxial sporangium is shaded darker gray. Inside of abaxial valve is shaded lightest gray. The serial dégagement demonstrated that part of the very convex abaxial valve was folded over the adaxial valve, nearly obscuring it. As it was more extensively revealed, the adaxial valve itself is vertically folded so that at most levels it appears two-parted, the fold being out of that plane. Adaxial valve entirely removed by dégaging in E. Scale bar = 1 mm. NMW 93.97G.51 ii.

Figure 6. *Sawdonia hippotheca* sp. nov. from Venezuela. Parts of fertile axes.

A. Axis fragment with 5 sporangia closely appressed to axis (arrows). Scale bar = 10 mm. NMW 93.97G.49b ii.

B. Detail of uppermost subopposite sporangia in Fig. 2A, showing each differently oriented and distorted. One on right was serially dégaged, stages of which are shown in Fig. 5. Scale bar = 2 mm. NMW 93.97G.51 ii.

C, D. Axis with lateral branch bearing a lateral sporangium to right fairly near its base. Lateral branch ends in an apparent circinate tip. D. Detail of the downwardly bent sporangium with broad stalk in C. Abaxial valve with two spines to right, outline of adaxial valve margin below (arrow). C. Scale bar = 5 mm. D. Scale bar= 2 mm. NMW 93.97G.49e.

Figure 7. *Sawdonia hippotheca* sp. nov. Interpretive drawing of compressed sporangium shown in Fig. 4B, to demonstrate the inside of the concave abaxial valve is in face view, surrounded by a narrow margin of outer valve and its spines. Scale bar = 1 mm. NMW 93.97G.46 ii.

Figure 8. *Sawdonia hippotheca* sp. nov. from Venezuela. Interpretation of position and orientation of sporangia in life.

Figure 9. *Sawdonia hippotheca* sp. nov. from Venezuela. Anatomically preserved specimen

A. Bifurcating axis, spines barely visible but 1-2 on upper left branch, with central dark strand which is permineralized in places. Region yielding material examined by SEM at arrow. Scale bar = 10 mm. NMW 93.97G.60, now destroyed.

B. Elongate xylem region of permineralized axis in Fig. 9A in transverse section view, polished section. Scale bar = 0.5 mm. NMW 93.97G.60.1.

C. Detail of polished section (Fig. 9B) showing differentially thickened, perforated wall (arrow). Scale bar = 50 μm. NMW 93.97G.60.1.

Figure 10. *Sawdonia hippotheca* sp. nov. from Venezuela. SEMs of xylem from permineralized strand. NMW 93.97G.60.2.

A. General view of some tracheids preserved in limonite, demonstrating the termination of one cell. Scale bar = 200 μm.

B. View of two types of pyrite/limonite preservation. To left, lumen casts showing grooves representing the position of the thickenings. To right, 'wall pyrite' replacing primary wall of the cells, including horizontal bars that represent pyrite filling the hollow insides of the thickenings. Scale bar = 50μm.

C. Detail of wall thickening with smooth surface of secondary wall, and pitlets on walls away from thickenings. Scale bar = 20μm.

D. Closeup of lumen cast. Arrow shows example where thickening may have become detached from lumen wall, therefore the thickening apparently burrows into lumen cast rather than being represented by a groove. Scale bar = 10μm.

Figure 11. *Sawdonia hippotheca* sp. nov. from Venezuela. Reconstruction of plant, showing our interpretation of location of two branching types and sporangia. Scale bar = 40 mm.

Table 1

Comparative data for *Sawdonia ornata*, *S. deblondii*, *S. hippotheca*.

Table 1

COMPARATIVE MORPHOLOGICAL DATA FOR SPECIES OF *SAWDONIA*

	Sawdonia ornata (Gaspé)	*Sawdonia deblondii*	*Sawdonia hippotheca* sp. nov.
Stem width (mm)	1.6-4.5	2.5 (5.2) 7.5	1-5.6 (most 4-5)
Spine length (mm)	0.9-3.9	1.7 (2.1) 2.7	3-5
Spine width at base (mm)	0.5-1.8	0.5 (1.2) 1.8	0.6-1
Spine base	slightly decurrent, tapered	slightly decurrent, triangular at base, then subulate	very decurrent, then more narrowly triangular
Spine shape/tip	tapered; some flared, incomplete, darkened at tip	apiculate or obtuse or truncated, may be slightly recurved abaxially	tapered, apiculate
Spine location	stems, sporangial stalk, abaxial valve of sporangium, smaller on sporangia	stems, sporangial stalk, abaxial valve of sporangium, smaller on sporangia	stems, sporangial stalk, abaxial valve of sporangium
Sporangium arrangement	approx. –sub-opposite/alternate	one side of axis, rarely at 90°	alternate, irregular, sub-opposite
Intersporangial distance (mm)	1.5-7	8-10	8-12
Sporangium shape	rounded	round to reniform	round-elliptical, slightly reniform?
Sporangium length (mm)	1.4-3.4	2.3-4.0	1.2-3
Sporangium width (mm)	1.4-3	2.3-4.5	
Stalk length (mm)	1.0-1.5	1.0-3.0	1.0-1.5
Stalk width (mm)	1-1.5 (ad); 0.2-0.8 (ab)	0.7-1 side view; narrower face view	1.3
Abaxial valve morphology	larger, slightly convex, extends over margin	larger, probably extends over margin	larger, deeply convex, probably extends over margin
Adaxial valve morphology	smaller, flat	more or less flat	more or less flat
Dehiscence zone	inwardly folded (both valves), narrow rim	two dark lines	thin dark band on both valves
Length spines on sporangia (mm)	0.2-0.8	similar or smaller than those of axis; no measurements given	2

Sporangium orientation	at about 50° angle, but often folded around axis	45-90° to axis, bent upwards	stalk departs at 90°, bends upward, downward or to side
Spores	unknown*	unknown	unknown
Epidermal features	elongate epidermal cells, stomata, papillae, "rosette" cell clusters	unknown	unknown
Branching pattern	pseudomonopodial; sometimes planar	rare, iso- to aniso-dichotomous, K-branching	broad dichotomy, lateral slightly constricted at base; and either subparallel or spreading; K-branching
Buds or probable arrested apices	present along axes, some abaxial close to branching point, circinately coiled laterals	sub-axillary	bumps rarely on lower side of lateral axis
Anatomy	elliptical exarch haplostele	elliptical exarch haplostele, G-type xylem	probably elliptical exarch haplostele, G-type xylem

NOTE. –Data from Berry and Gensel (2016), Gerrienne (1996) and this paper.

* Spore description in Hueber, 1971, but source (Gaspé or Abitibi River) unknown; spores of *S. acanthotheca* described (Gensel, 1980) but this taxon is excluded from *Sawdonia* by these authors.

Figure 1

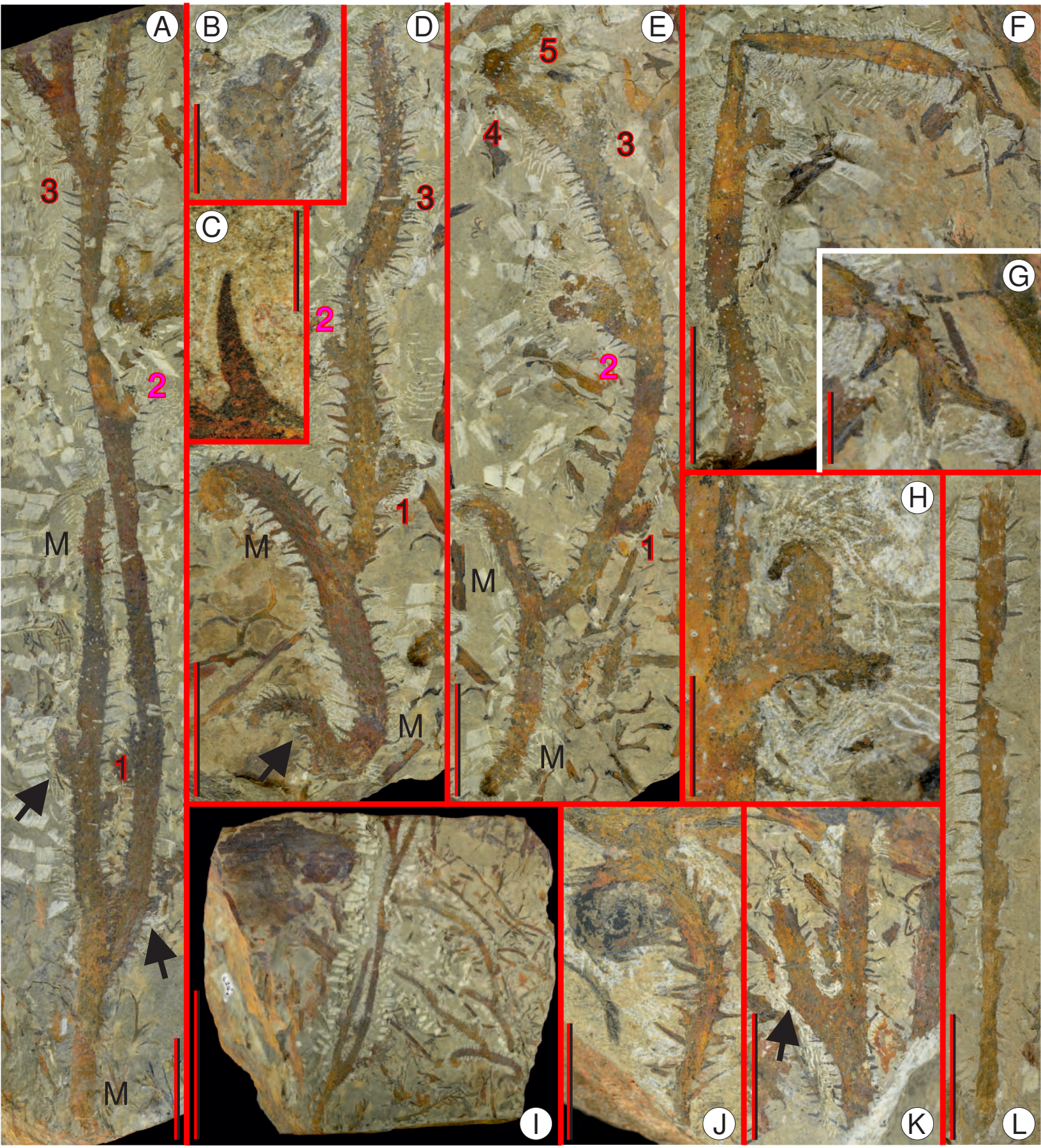
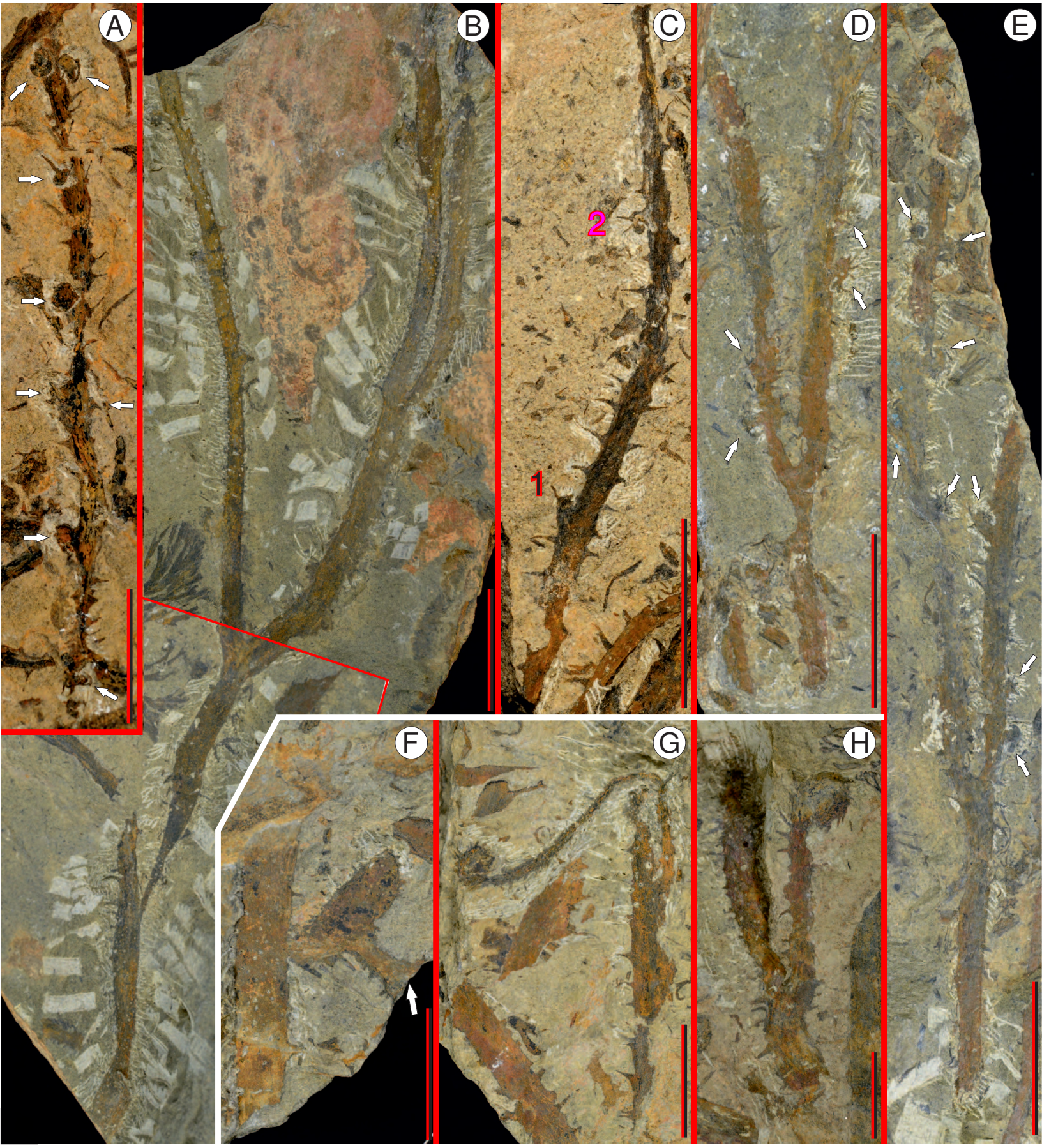


Figure 2



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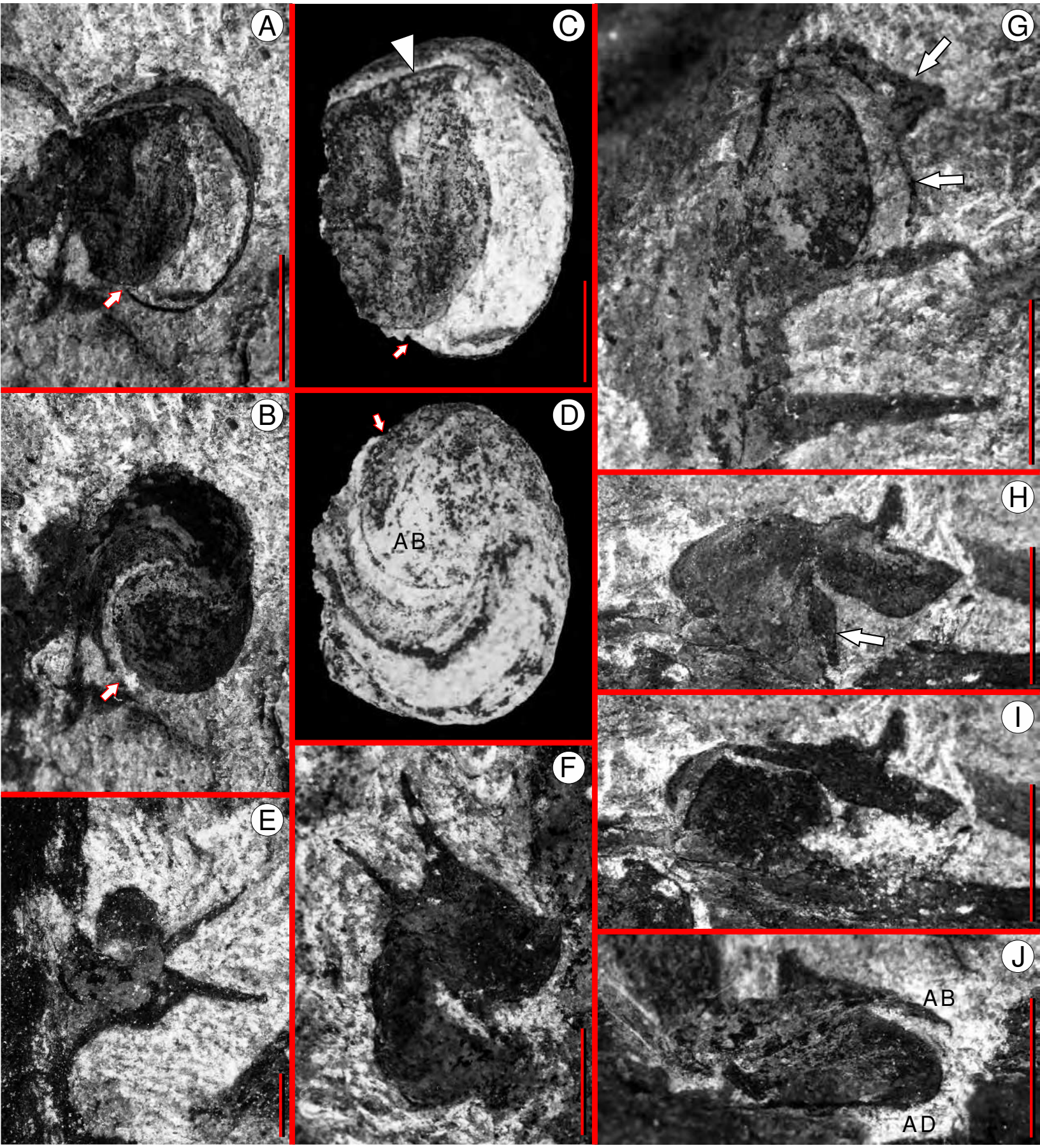

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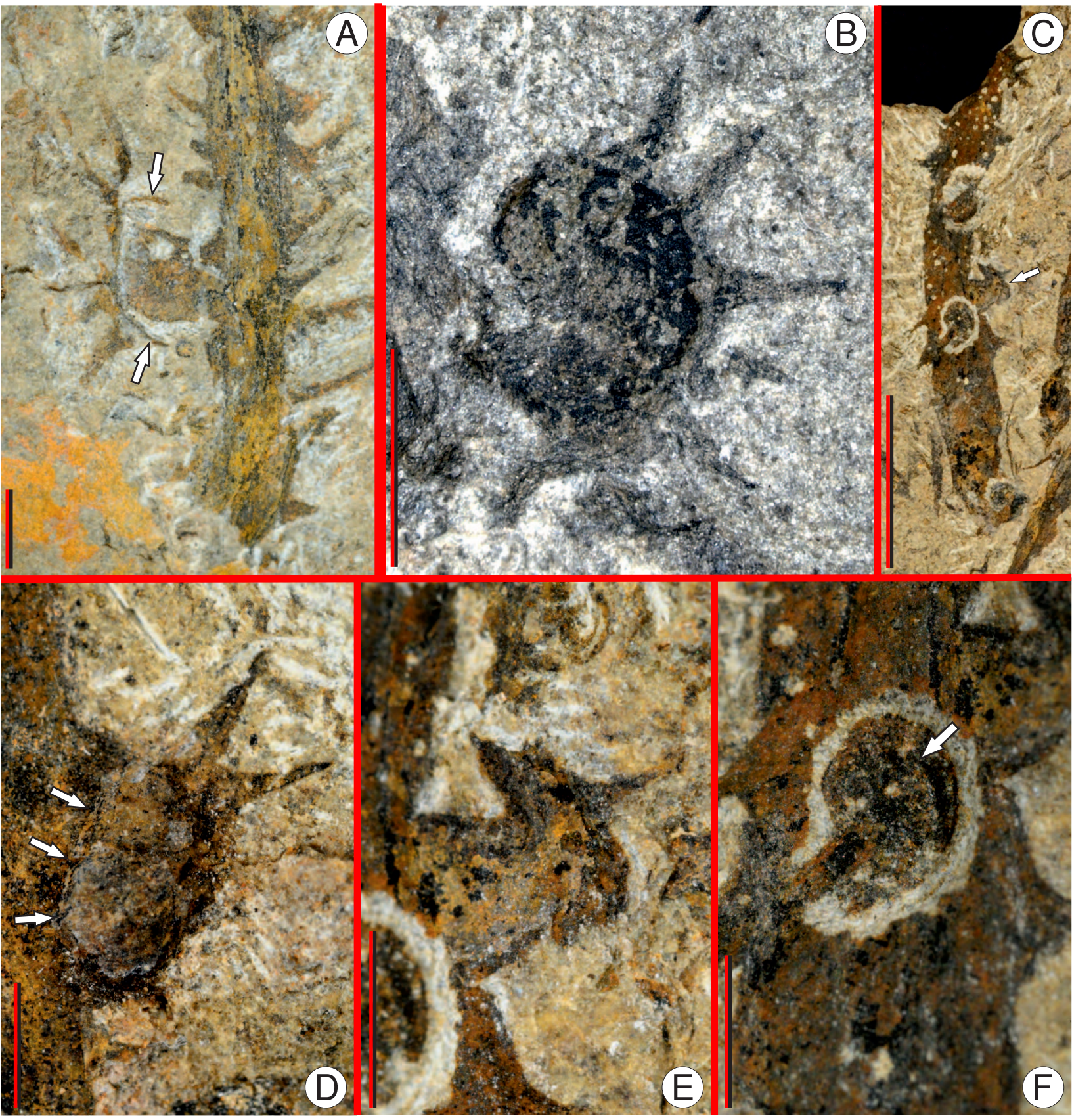

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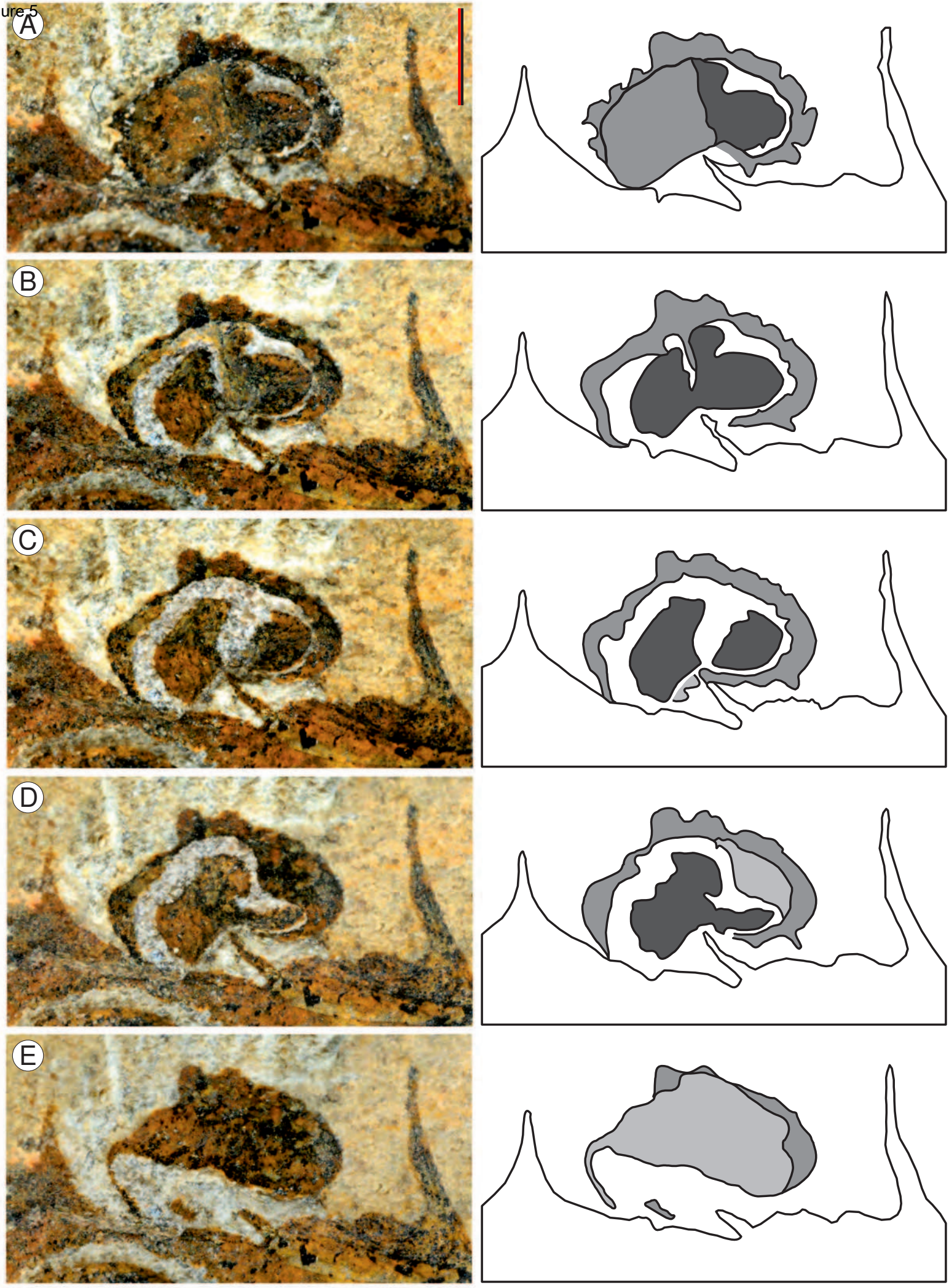

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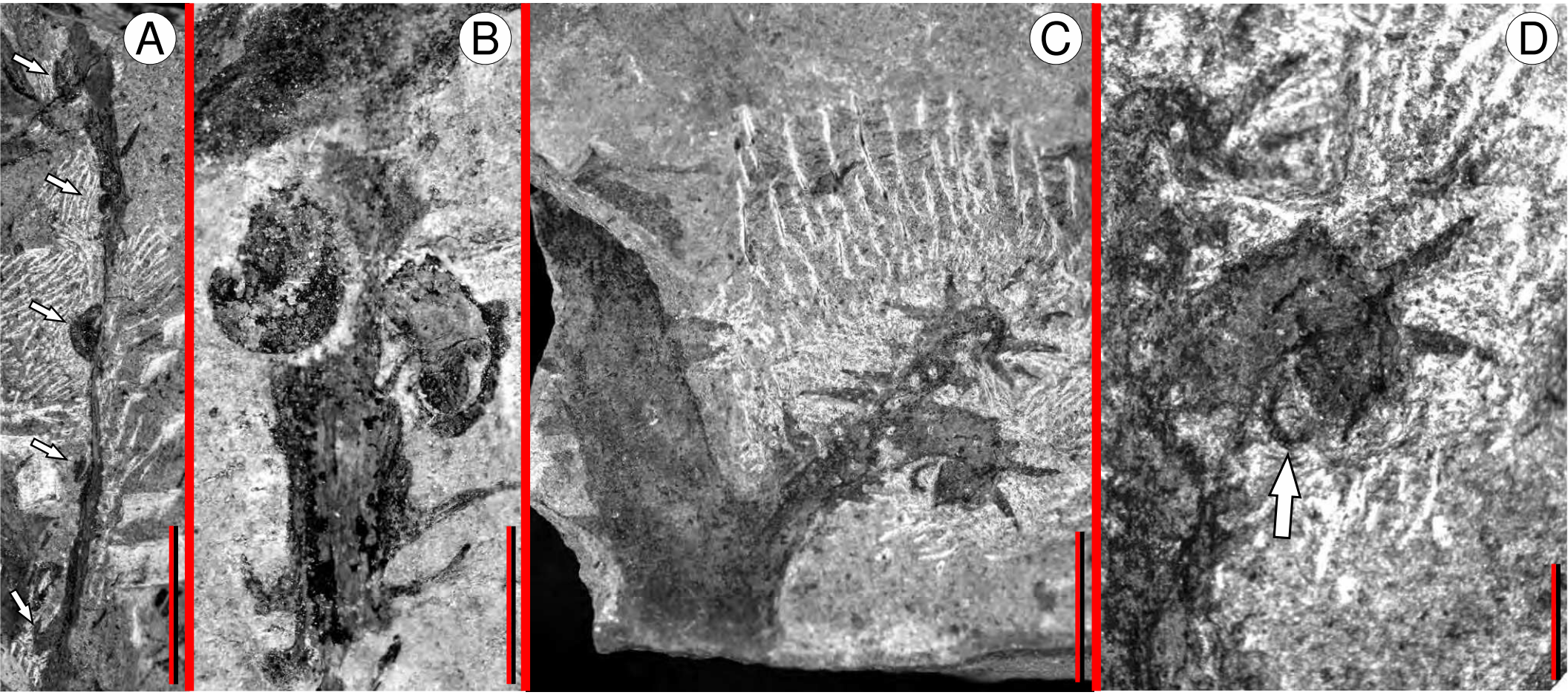

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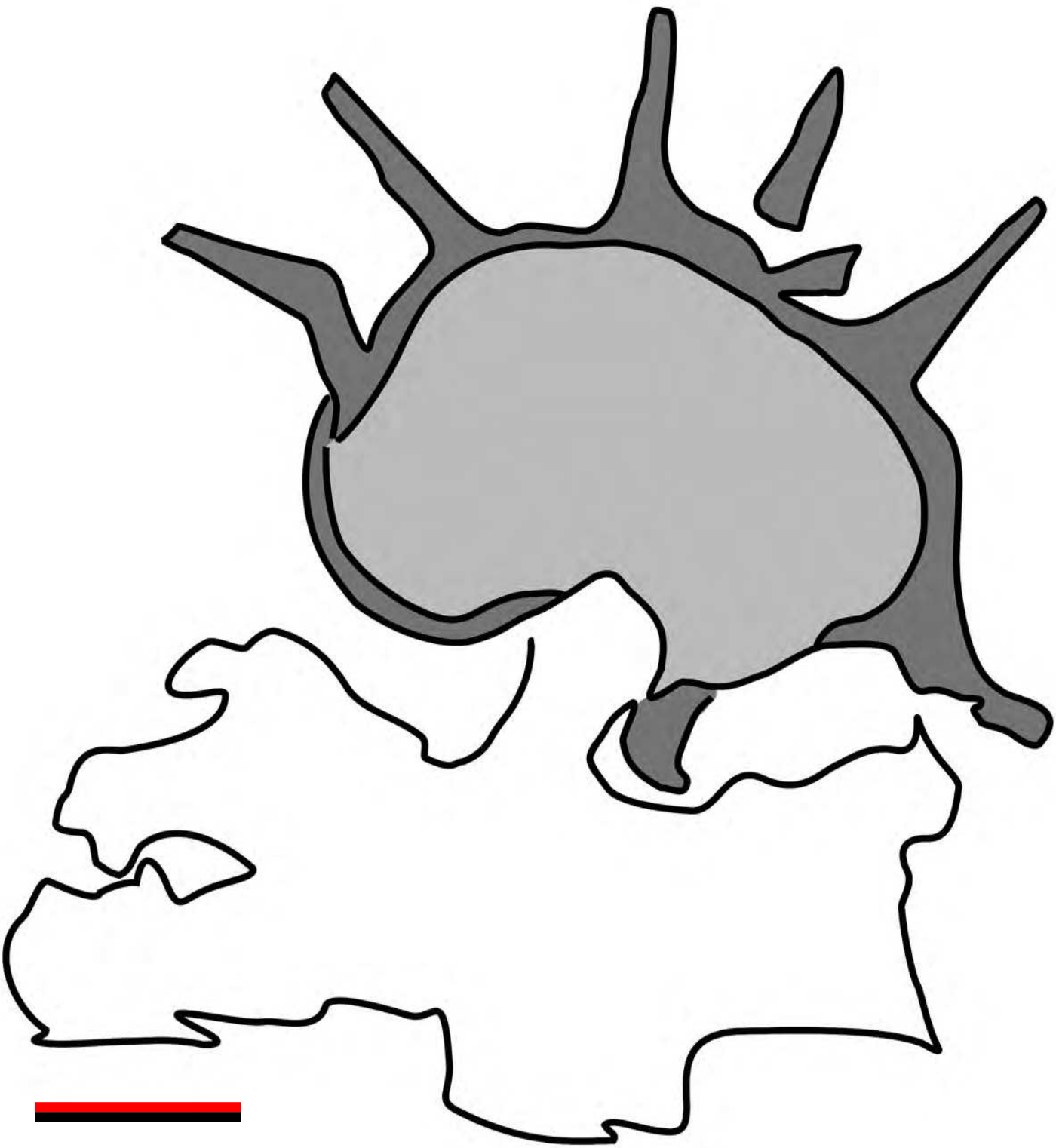

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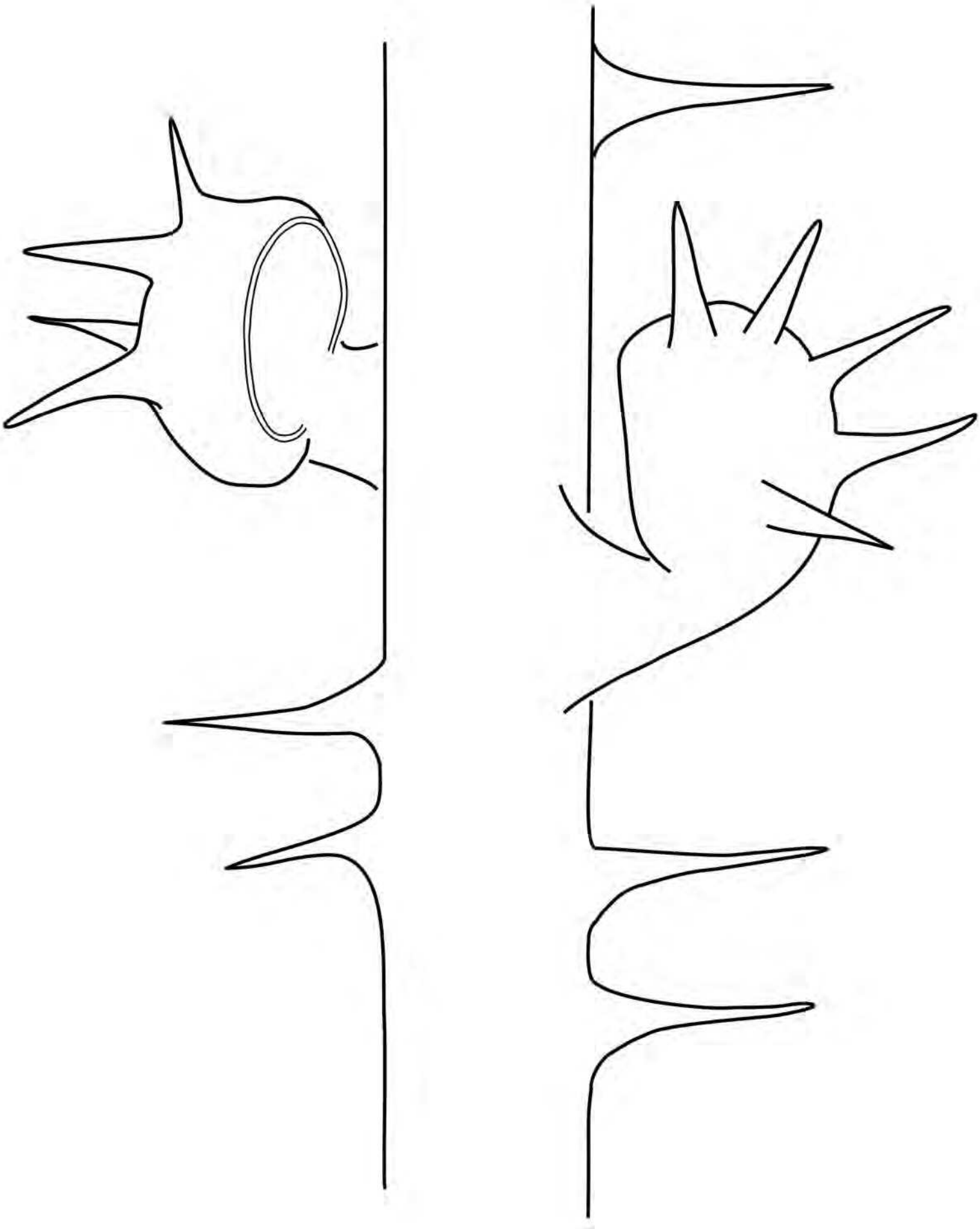

Fig

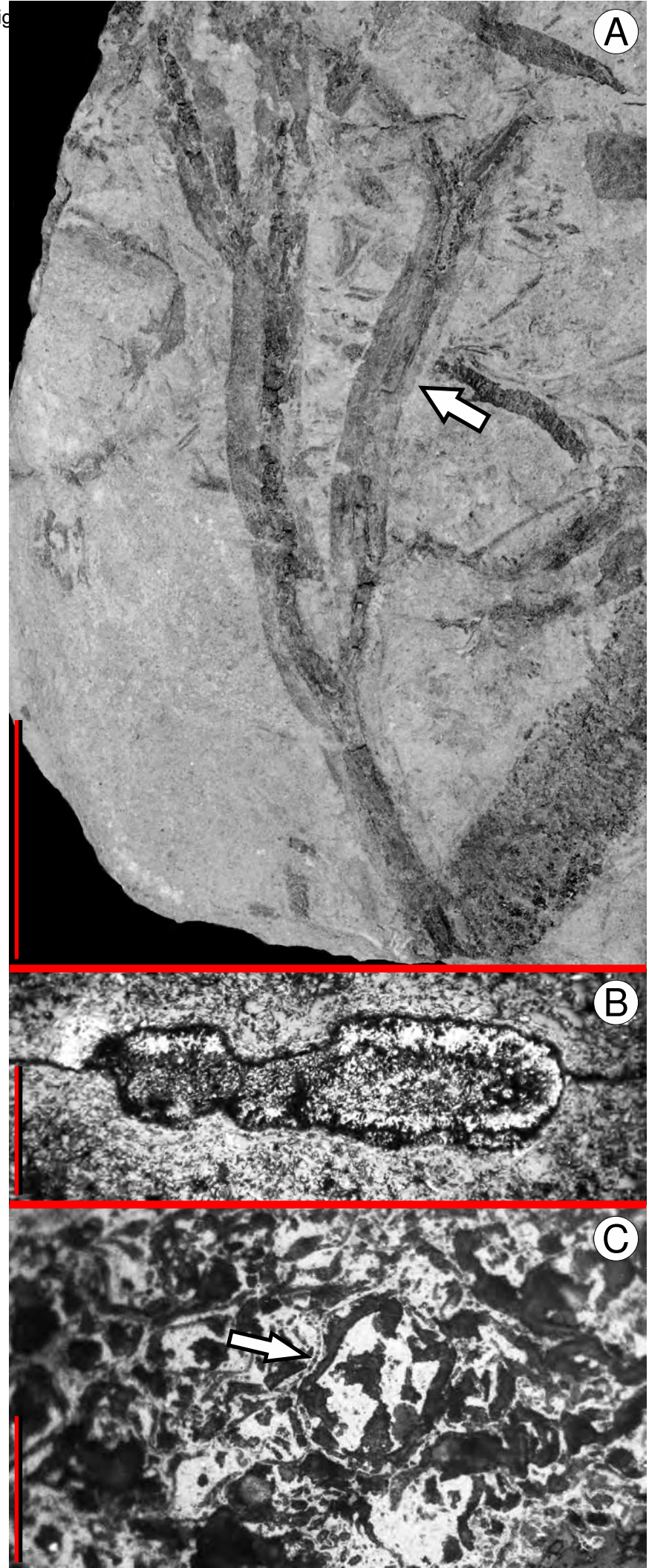

Figure 10

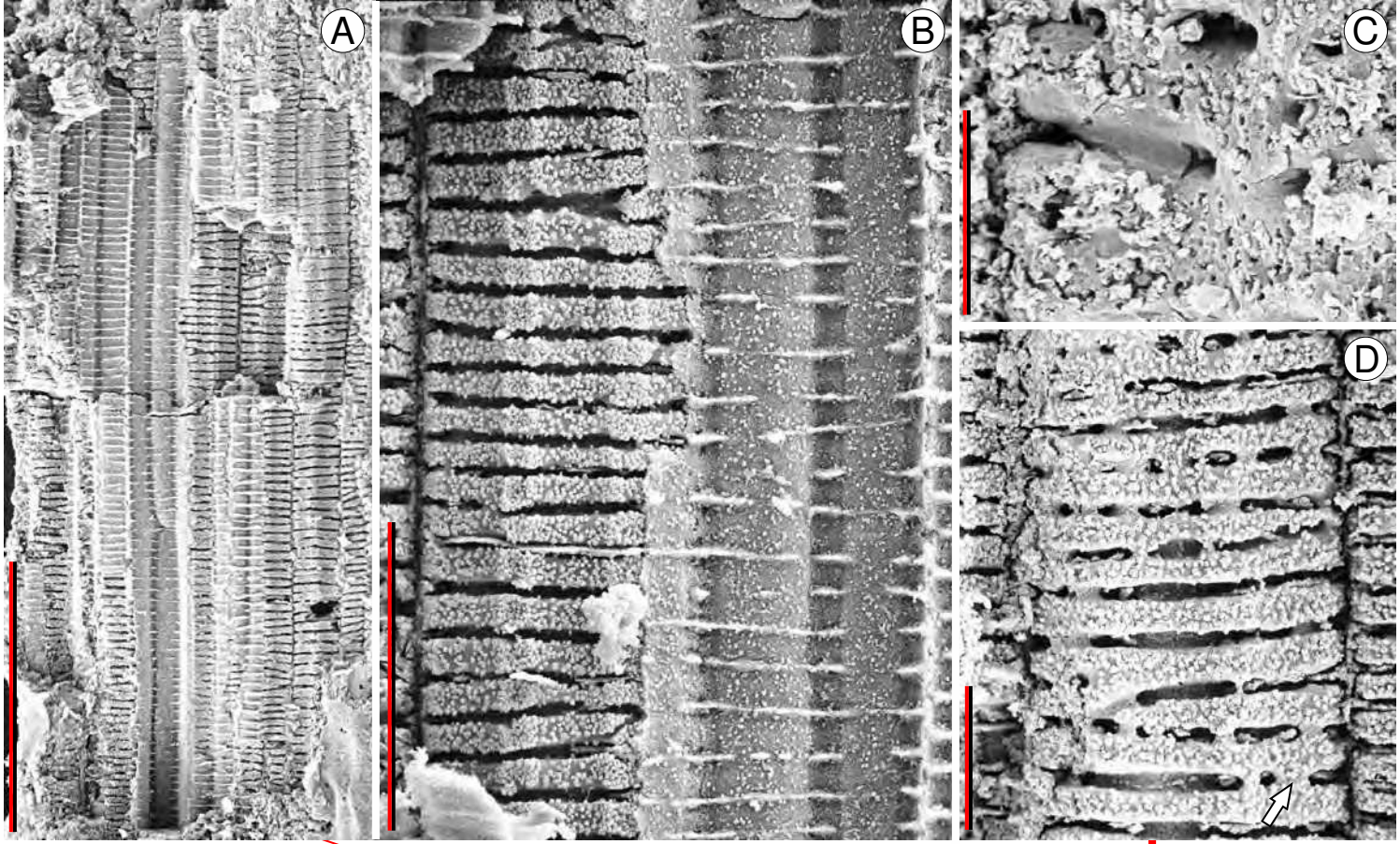

Figure 11